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Proline Content in Leaves of Eggplant, *Solanum Melongena*: Analysis of Genetic Determinism and Correlation with Agro-Morphological Traits

Kouassi Abou Bakari[1*], Kouassi Koffi Brice Aymar[1], Kouadio Koffi Alfred[1], Tiecoura Kouakou[1], Kouassi Auguste[1], Prohens Jaime Tomas[2], N'guetta Assanvo Simon-Pierre[1]

[1]Laboratoire de génétique, UFR-Biosciences, Université Félix Houphouët-Boigny (UFHB), 22 BP 582 Abidjan 22
[2]Instituto de Conservación y Mejora de la Agrodiversidad Valenciana, UniversitatPolitècnica de València, Camino de Vera 14, 46022 Valencia, Spain

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***Corresponding author:** Kouassi Abou Bakari

Abstract

Original Research Article

For an efficient and sustainable development of agriculture, it is necessary to obtain plant material which can face new environmental constraints due to climate change. The present study analysed the genetic determinism of proline content, an amino acid, marker for stress resistance, and its correlation with agro-morphological characteristics in *S. melongena* and *S. insanum*. Plant material consists of eggplant accessions MEL1 and MEL5, *S. insanum* accession INS1, two interspecific F1 hybrid progenies and two backcross progenies. Proline content was estimated using young leaves collected in the morning. Genetic determinism of proline content was analysed based on the segregation pattern in BC1 progenies. Phenotypic and genotypic coefficients of correlation between proline content and 16 agro-morphological traits were estimated. Proline content had a continuous and transgressive distribution in BC1 progenies, "(MEL1 x INS1) x MEL1" and "(MEL5 x INS1) x MEL5", which suggests that it has a polygenetic control. In addition, the gap between genotypic and phenotypic coefficients of variation was small whereas the narrow sense heritability was moderate; indicating that non-additive genetic effects such as dominance and / or epistasis effects may be involved in the expression of proline content. High negative correlations were observed between proline content and fruit characteristics, suggesting that they could be used as phenotypic markers for assessing the ability of eggplant genotypes to produce larger or smaller quantities of proline. These data also show that any eggplant breeding programme aiming to increase drought tolerance by increasing proline content in the leaves may lead to the selection of varieties with small fruits.

Keywords: Genetic correlation, heritability, Proline content, *Solanum melongena*, *S. insanum*, transgressive segregation.

INTRODUCTION

Eggplant, *Solanum melongena* is a herbaceous plant of the Solanaceae family. It is grown for its fruits and leaves that are used in various food recipes [1]. It is the third most important cultivated Solanaceae species after potato, *Solanum tuberosum*, and tomato, *Solanum lycopersicum*. According to statistics from the United Nations Food and Agriculture Organization (FAO), global production of eggplant was estimated at just over 52,3 million tonnes in 2016 for a total area of around 1.8 million hectares. China and India are the main producers with respectively 32 million and more than 12.5 million tonnes in 2016. [2]. In Africa, eggplant production has been estimated at 1,712,753 tonnes on an area of 107,547 hectares. However, in recent years there has been a decline in crop yield and productivity due to the effects of climate change. Indeed, climate change induces mainly modification of rainfall and temperature. Increasing temperatures and changes in rainfall patterns above a certain threshold have direct effects on crop yields [3]. In Ivory Coast, from 1960 to 2010, the temperature increased on average by 1.6 ° C and rainfall decreased by 28.9% and 7.7% in the southern in the northern regions, respectively; resulting in a decrease in agricultural productivity. Therefore, producers have modified planting schedules in order to escape or mitigate the effects of the new environmental constraints [4]. In this context, it is essential to create plant material with genotypic combinations that can meet these new challenges and ensure the efficiency and sustainability of agriculture. In this respect, *S. insanum*, the closest wild relative of *S. melongena*, is found in a wide range of climatic conditions [5-7]. It has been mainly subjected to natural selection and has therefore not suffered a bottleneck due to domestication and artificial selection by breeders. This species therefore may have a greater allelic diversity of genes controlling agronomic traits of interest and could play a major role in eggplant breeding for adaptation to the effects of climate change such as drought.

Thus, interspecific hybridizations and backcrosses allowed the introgression of *S. insanum* genes in *S. melongena* [8, 9]. However, selection of the obtained hybrid progenies requires their characterization using agro-morphological descriptors as well as protein and molecular markers. It is the reason why this study analyzed the genetic determinism of proline content, an amino acid, marker of plants' drought resistance [10], and its correlation with agro-morphological characteristics, in two accessions of *S. melongena*, one accession of *S. insanum*, their interspecific F1 progenies and their first backcross progenies. The objective is to identify at least one agro-morphological descriptor strongly correlated with proline content in the leaves and which could be used as a phenotypic marker of a potential drought tolerance ability of eggplant varieties

MATERIALS AND METHODS

Site of the Study

This study was carry out in Ivory Coast, on an experimental plot of the research station of the National Center for Agronomic Research (CNRA), located 17 km from Abidjan. The geographic coordinates of the plot are latitude 5° 19' 516" N, longitude 004° 08' 206" W and an elevation of 37 m above sea level. The climate of the site is characterized by 2 rainy seasons and 2 dry seasons. The great rainy season covers the period from April to July while the great dry season runs from December to April with the lowest rainfall recorded in January. Average monthly temperatures range from 25.1 to 29.3°C. The hottest period is from January to April and the coolest period is from July to September.

Plant Material

The plant material was consisted of: 1) the accessions BBS-118/B and 8104 of eggplant, *S. melongena*, which were coded respectively MEL1 and MEL5; 2) the accession SLKINS-1 of *Solanum insanum*, coded INS1. 3) Two F1 progenies of the accession INS1 and the accessions MEL1 and MEL5, respectively. The accessions M1 and M5 were used as female parents for these interspecific hybridizations. 4) Two backcross progenies of the F1 hybrids and the accessions MEL1 and MEL5, respectively. F1 hybrids were used as female parents for the backcrosses.

METHODS

Treatments and Planting Design

According to the protocol developed by [11], the seeds were soaked for 24 hours in water and then in a solution of 500 ppm gibberellic acid for 24 hours. They were subsequently sown in Petri dishes containing cotton or paper soaked in 1000 ppm potassium nitrate solution. In case the seeds were sown directly in peat or another substrate, they were watered with 1000 ppm potassium nitrate solution for one week. The seedlings were kept in the nurseries for 45 days and then 5 plantlets of each parental accession and each F1 progeny as well as 50 Individuals of each BC1 progeny were transplanted onto the field during the great rainy season in a randomized complete block design with a spacing of 1.5 and 1 m, respectively between and within rows. The plants were treated with the fungicide "Ivory 80 WP" (Composition: Mancozeb 80 g / kg) and the insecticide "Cypercal 50 EC" (composition: Cypermethrin 50 g / L) at the rates of 2kg / ha and 1 L / ha, respectively when pests attacks were observed. In addition, the plot was regularly weeded.

Measurement of agro-morphological characters

The plants were characterized with 16 agro-morphological characters including 7 vegetative growth characters and 9 yield related traits (Table-1) derived from eggplant descriptor [12]. Vegetative growth characteristics were measured when the first flower was observed. Flowering characteristics were assessed on 3 to 4 randomly selected inflorescences per plant. When the inflorescence consists of more than 3 flowers, the number of stamens was counted on 3 flowers also chosen at random. Fruit characteristics were measured on 3 to 4 fruits per plant.

Table-1: Agro-morphological characters mesured on parental accessions and interspecific hybrid progenies

N°	Character	Unity (IS)	Code	Type of character
1	Plant Height	cm	PLHE	Vegetative Growth traits
2	Plant Canopy Width	cm	PLWI	
3	Ramification Index	—	RAM	
4	Leaf Blade Length	cm	LBLE	
5	Leaf Blade Width	cm	LBWI	
6	Petiole Length	cm	PELE	
7	Petiole Diameter	mm	PEDI	
8	Number of Flowers/Inflorescence	—	NFLIN	Yield related traits
9	Style Length	mm	STLE	
10	Number of stamens	—	NBST	
11	Fruit Length	cm	FRLE	
12	Fruit Width	cm	FRWI	
13	Fruit Pedicel Length	mm	FRPL	
14	Fruit Pedicel Diameter	mm	FRPD	
15	Fruit Weight	g	FRWE	

IS : International System

Determination of proline content

Young leaves were collected preferentially in the morning. The collected leaves were wrapped in aluminum foil and placed in ice for transfer to the laboratory where the samples were stored in the freezer at -20°C. Proline was extracted from the leaves according to the protocol described by Chen and Zhang [13]. Proline concentrations (C) in the different leaves samples were calculated according to the following formula:

$$C = K * OD.$$

Where,

K is the coefficient obtained from a calibration curve plotted using a series of proline solutions of known concentrations

OD is the optical density of the supernatant of each crushed leaves sample.

Data Analysis

Analysis of Variance and Normality Tests

One-way analyse of variance (ANOVA) was performed to test the effect of plant type (MEL1, MEL5, INS1, F1 and BC1) on phenotypic values of each agro-morphological character. Duncan's Multiple Range Test (MRT), at 5% significance threshold, was used to range phenotypic mean values of parental accessions and F1 and BC1 progenies. Kolmogorov-Smirnov and Shapiro-Wilk tests, at 5% significance threshold, were used for normality test of proline content in BC1 progenies. These statistical analyses were performed using the Microsoft Office spreadsheet, Excel 2013 and IBM SPSS Statistics 22.0 software (IBM Corp. Armonk, NY, USA).

Estimation of variance components and genotypic and phenotypic correlations

Estimates of additive genetic variance and phenotypic variance were computed using a mixed linear model based on the “animal genetic model” and the restricted maximum likelihood method [14]. Variances/co-variances’ matrices as well as genotypic and phenotypic correlations matrices were calculated with the Variance Components Estimation (VCE) package, version 6.0.2 [15]. The VCE 6.0.2 package also provides the additive (r_a) and phenotypic (r_p) genotype correlation coefficients, respectively.

The formula for calculation of the correlations is: $\mathbf{r} = \frac{\mathbf{cov\ (x,y)}}{\sqrt{\sigma_x^2 \ x\ \sigma_y^2}}$.;

Where,

cov (x, y) is the covariance between 2 characters x

y, σ^2_x and σ^2_y are variances of characters x and y, respectively.

RESULTS

Comparison of proline contents of parental accessions and F1 progenies.

Proline contents of parental accessions and F1 progenies were significantly different ($P < 0.05$). Proline contents of the accessions MEL5 and INS1 were statistically similar and they were higher than that of the accession MEL1. Proline contents of both F1 progenies, “MEL1 x INS1” and “MEL5 x INS1” were statistically similar. On the other hand, they were higher than those of their respective parents (Table-2).

Table-2: Mean values and standard deviations of proline content in parental accessions and F1 and BC1 progenies

Generations	Accessions	N	Mean ± SD (µl/ml)
P	MEL1	3	0.82 ± 0.05^{a}
	MEL5	3	$1.71 \pm 0.52^{b\ c}$
	INS1	3	$1.61 \pm 0.45^{b\ c}$
F1	MEL1 x INS1	3	2.20 ± 0.21^{c}
	MEL5 x INS1	3	2.15 ± 0.13^{c}
BC1	(MEL1 x INS1) x MEL1	50	0.77 ± 0.31^{a}
	(MEL5 x INS1) x MEL5	50	$1.04 \pm 0.65^{a\ b}$
F	—	—	9.308
P-value	—	—	0.000*

P: parental accessions, F1: interspecific hybrid; BC1: first generation backcross; Mean: mean value, SD: standard deviation; N: number of observations; F: value of the statistic associated with the Fisher test; P-value: probability value associated with the Fisher test. Mean values indexed with the same letter are not statistically different according to Duncan Multiple Rang Test at 5% significance threshold

Distributions of proline content in BC1 progenies

Kolmogorov-Smirnov and Shapiro-Wilk normality tests revealed that proline content has a normal ($P < 0.05$) but asymmetric distribution in the BC1 progeny "(MEL1 x INS1) x MEL1". In contrast, proline content in the BC1 progeny "(MEL5 x INS1) x MEL5" was not normally distributed ($P > 0.05$) (Table-3 and Figure-1). On average, proline content in the BC1 progeny "(MEL1 x INS1) x MEL1" was statistically similar to that of the accession MEL1. However, proline content has a transgressive segregation in both BC1 progenies. Indeed, proline content of all the individuals in the BC1 progeny "(MEL1 x INS1) x MEL1" were lower than that of the F1 progeny "MEL1 x INS1". On the other hand, the accession MEL1 has a median position compared to those of the descendants "(MEL1 x INS1) x MEL1". Proline contents of the hybrid "MEL5 x INS1" and the accession MEL5 were higher than those of most the individuals in the BC1 progeny "(MEL5 x INS1) x MEL5".

Table-3: Normality tests for the distribution of proline content in the BC1 progenies

Test		(MEL1 x INS1) x MEL1	(MEL5 x INS1) x MEL5
Kolmogorov-Smirnov	Statistic	0,145	0,108
	df	49	49
	P-value	0,010	0,200
Shapiro-Wilk	Statistic	0,933	0,960
	df	49	49
	P-value	0,007	0,086

df: degree of freedom, P-value: value of error probability associated to the statistical test.

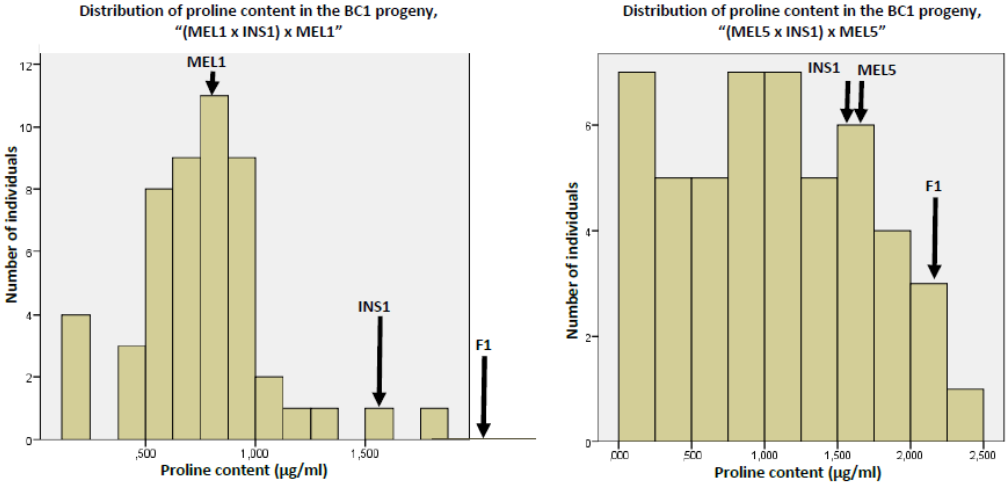

Fig-1: Distribution of proline content in BC1 progenies

The vertical arrows indicate the positions of mean values of parental accessions MEL1, MEL5 and INS1 as well as F1 hybrid progenies with respect to the BC1 progenies

Genotypic and phenotypic correlations between proline content and agro-morphological

In general, very low to near-zero genotype and phenotypic correlation coefficients were observed between proline content and vegetative growth characteristics. Flowering time was not correlated with proline content. The other yield related traits were negatively correlated with proline content. Genotypic correlations were very low with the number of flowers per inflorescence, style length, number of stamens, fruit length and fruit pedicel length. On the other hand, genotypic correlations were moderate with fruit weight; high with fruit width and fruit pedicel diameter. Phenotypic correlations were low with the number of flowers per inflorescence and style length; moderate with the number of stamens, fruit length, fruit pedicel length and fruit weight; high with fruit width and fruit pedicel diameter (Table-4).

Table-4: Additive genetic variance (σ^2_a) and phenotypic variance (σ^2_p), Mean values of agro-morphological characters (μ) and genetic (r_a) and phenotypic (r_p) correlations with proline content

Traits	σ^2_a	σ^2_p	μ	r_a	r_p
Vegetative growth trait					
PLHE	29.35	39.20	65.86	0.059	-0.045
PLWI	175.25	227.30	130.12	-0.051	-0.110
RAM	1.59	3.40	6.48	0.088	-0.066
LBLE	64.08	80.90	19.69	0.186	0.142
LBWI	38.09	76.00	14.35	0.018	0.081
PELE	12.80	49.20	7.80	0.026	-0.425
PEDI	0.61	7.30	4.44	-0.094	-0.548
Yield related trait					
FLTI	40.90	52.10	78.38	0.001	-0.003
NFLIN	0.41	2.80	2.46	-0.185	0.373
STLE	9.59	31.10	2.13	-0.145	-0.268
NBST	0.63	2.00	5.12	-0.119	-0.478
FRLE	98.80	243.10	6.84	-0.393	-0.519
FRWI	6.46	27.10	4.63	-0.737	-0.717
FRPL	13.07	41.80	3.93	-0.283	-0.43
FRPD	42.34	126.40	7.21	-0.778	-0.829
FRWE	13480.33	35234.80	99.81	-0.577	-0.508
Proline content	1.01	2.40	1.47		
Plant Height (PLHE), Plant Canopy Width (PLWI), Ramification index (RAM), Leaf Blade Length (LBLE), Leaf Blade Width (LBWI), Petiole Length (PELE), Petiole Diameter (PEDI), Flowering Time (FLTI), Number of Flowers/Inflorescence (NFLIN), Style Length (STLE), Number of Stamens (NBST), Fruit Length (FRLE), Fruit Width (FRWI), Fruit Pedicel Length (FRPL), Fruit Pedicel Diameter (FRPD), Number of Fruits/Infructescence (NFRIN), Fruit Weight (FRWE)					

DISCUSSION

Proline contents of the accessions MEL5 of *Solanum melongena* and INS1 of *S. insanum* were statistically similar whereas they were higher than that of the accession MEL1. This difference in proline content in parental accessions could be explained by the fact that they originate from different ecological conditions. Indeed, accessions MEL5 and INS1 are both from Sri Lanka while accession MEL1 is from Côte d'Ivoire. Moreover, considering accessions MEL1 and MEL5, the difference in proline content could be determined by genetic differences. Indeed, accession MEL1 belongs to the "western" genetic group whereas accession MEL5 belongs to the "eastern" genetic group [16, 17]. Accumulation of proline in plants' leaves and stems in response to environmental constraints such as salinity and water deficit has been reported by several authors [10, 18, 19]. However, significantly different proline contents have been observed in 3 bean (*Vicia faba* L.) lines in absence of any stress and also under the effect of increasing sodium chloride (Nacl) concentrations [20]. Since proline concentration is an indicator of plant tolerance to environmental stress [10, 21-23], our results suggest that higher proline concentrations in accessions MEL5 and INS1 might give them better drought tolerance abilities compare to accession MEL1.

Segregation of proline content was transgressive in both BC1 progenies "(MEL1 x INS1) x MEL1" and "(MEL1 x INS1) x MEL1". These data illustrate the complexity of the genetic determinism of proline content. Indeed, transgressive segregation is determined by super-dominance effects, rare alleles, epistatic interactions, complementary or antagonistic genes in interspecific and intraspecific hybrid progenies [24-26]. Moreover, the transgression is all the more observed for different traits that individuals belonging to the same species or to genetically close species are crossed and they reproduce in particular by autogamy. Thus, since *S. insanum* is the wild progenitor of *S.*

melongena [5, 27] and, the two species reproduce mainly by autogamy [28], hybridizations of their accessions may have favoured allelic combinations that induced the transgressive segregation of proline content observed in the two BC1 progenies

Proline contents in interspecific F1 progenies were significantly higher than those of their respective parents. There is therefore a heterosis effect in F1 progenies for the expression of proline content, which could also be explained by the fact that parental accessions are mainly autogamous [28]. This mode of reproduction gives them a high rate of homozygosity for a large number of characters that favours heterosis in hybrid F1 progenies. Indeed, when homozygous lines are crossed, the heterozygosity can increase the vigour of the hybrid [29]. Similar heterosis effects have already been obtained for different vegetative growth characteristics [9, 30].

Very low genotypic and phenotypic correlation coefficients were observed between proline content and most of the studied agro-morphological traits. To our knowledge, this study is the first that deals with genotypic and phenotypic correlations between agro-morphological characteristics of a crop plant and proline content. As reported by many authors [10, 22], the low values of correlation coefficients may be explained by the fact that the synthesis of proline is all the higher as growth is greatly reduced due to stress. Accumulation of proline in plant organs is said to contribute to the protection of enzymatic and membrane systems to allow the continuation of physiological and biochemical processes under severe drought conditions [10, 31]. Therefore, in absence of any stress, as it was the case in the current study, since the expression of the genes responsible for growth and development of plant organs is favoured, their characters appear uncorrelated, or even negatively correlated with proline content in the leaves. However, strong negative correlations between proline contents and fruit width and fruit pedicel diameter suggest that they could be used as phenotypic markers for assessing the ability of eggplant genotypes to secrete larger or smaller amounts of proline and to be therefore more or less tolerant to drought. In addition, any breeding program aiming to improve tolerance or resistance to drought of eggplant varieties by increasing proline content in the leaves may lead to the selection of varieties with small fruits.

CONCLUSIONS

Data from this study suggest that expression of proline content in eggplant leaves has complex genetic determinism which may involve non-additive genetic effects such as dominance and / or epistasis effects. There were also strong negative correlations between proline content and fruit width as well as fruit pedicel diameter suggesting that they could be used as phenotypic markers for assessing predisposition of eggplant genotypes to secrete more or less important quantities of proline. However, any eggplant breeding program aiming to increase the ability of drought tolerance through increased proline production could lead to the selection of varieties with small fruits.

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